The vegetation of Brazilian 'murundus' – the island-effect on the plant community

ARY TEIXEIRA DE OLIVEIRA-FILHO

Departamento de Ciências Florestais, Escola Superior de Agricultura de Lavras, 37200, Lavras, MG, Brazil

ABSTRACT. The 'campos de murundus' (earthmound fields) are typical landscapes of the cerrado (savanna) region of Central Brazil and are characterized by many rounded earthmounds called 'murundus' which are scattered over a grassland surface. As these areas are normally liable to seasonal water-logging, the earthmounds are true habitat islands capable of bearing woody plants typical of the cerrado, which are normally very intolerant of root inundation. The vegetation of an area of murundus field at Cuiabá, in the State of Mato Grosso, Central Brazil, was surveyed for the purpose of evaluating the island-effect on the plant community growing on the mounds/islands. Two main aspects were considered: the influence of the size of the mound and the differences between the types of cerrado occurring on the mounds and on the areas surrounding the murundus field. Most plant species occurring on the mounds were also present in the flora of the surrounding cerrado. However, only a fraction of these species was able to colonize the mounds successfully. The number of species on the mounds was found to be significantly correlated with mound area. Species-area relationships were better described with the power model $S = C(A^z)$ than with the exponential model $S = C + z$ (logA) (fitted with linear regression). The mound size also had a strong influence on the spatial distribution of the species on the surface of the mounds. The species were organized in an increasing number of concentric topographic belts corresponding to a gradient of soil depth above the flooding level.

RESUMO. (A vegetação dos murundus do Brasil Central – o efeito ilha sobre a comunidade vegetal). 'Campos de murundus' são paisagens típicas da região do cerrado, no Brazil Central, caracterizadas por incontáveis montes de terra arredondados, os murundus, que se acham distribuídos sobre a superfície de um campo. Como estas áreas são normalmente sujeitas a excesso hídrico estacional, os murundus tornam-se verdadeiras ilhas ecológicas capazes de abrigar plantas lenhosas de cerrado, as quais são normalmente muito intolerantes à saturação hídrica no solo. A vegetação de uma área de campo de murundus em Cuiabá, Mato Grosso, foi inventariada com o propósito de avaliar o efeito ilha na comunidade vegetal que cresce sobre os murundus/ilhas. Dois aspectos principais foram considerados: a influência da área do murundu e as diferenças e semelhanças entre o cerrado dos murundus e o cerrado das áreas circunvizinhas ao campo. A maioria das espécies de plantas dos murundus também foi encontrada no cerrado circunvizinho. Contudo, apenas uma parte destas espécies demonstrou capacidade para colonizar com sucesso os murundus. Foi encontrada uma significativa correlação entre o número de espécies de plantas e a área do murundu. As relaçoes espécie-área foram melhor descritas pelo modelo log-log; $S = C(A^z)$; do que pelo modelo exponencial; $S = C + z$ (logA) (ajustados por regressão linear). O tamanho das ilhas demonstrou exercer também uma grande influência na distribuição espacial da comunidade vegetal. As espécies se mostraram organizadas em um número crescente de anéis topográficos concêntricos correspondentes a um gradiente de profundidade do solo acima do nível das inundações.

KEY WORDS: Brazil, cerrado, savanna, murundus, island biogeography.

INTRODUCTION

The 'murundus' are rounded earthmounds (0.3–20.0 m in diameter and 0.2–2.0 m in height) which are found scattered over some grasslands and less frequently under woodlands and gallery forests of the cerrado (savanna) region of Central Brazil. The landscapes known as 'campos de murundus' (literally 'earthmound fields') occur mostly in grasslands liable to seasonal water excess caused by an outcropping water table or by flooding. Thus, when the surrounding grasslands are saturated or inundated, the earthmounds are 'islands' capable of bearing woody plants typical of the cerrado, which are normally very intolerant of water-logging (Oliveira-Filho & Martins 1991).

The origin of these campos de murundus has been a controversial issue. In some cases they have been associated with differential erosion processes (Diniz de Araujo Neto *et al.* 1986, Furley 1986). Others have proposed an origin linked with the localized activity of termites (Mathews 1977, Oliveira-Filho 1992). In fact, these landscapes are now known to originate from more diverse phenomena than previously thought (Oliveira-Filho & Furley 1990).

An area of campo de murundus near Cuiabá, State of Mato Grosso, central-western Brazil, was described in detail in a previous paper (Oliveira-Filho 1992) and this area was considered as providing evidence for the termite-origin hypothesis, particularly in the case of the 'floodplain murundus'. That study took the view that this particular type of earthmound was formed mainly by the accumulation of soil caused by localized termite activity. The nest building of termites followed by nest degradation for several generations of colonies results in the formation of a pediment around the termitaria. The formation of the murundus can be regarded as a primary succession process determined by the expansion of these habitat islands as more soil is cumulatively added to the mound.

The present study deals with the vegetation of the earthmounds of the same area reported in Oliveira-Filho (1992). The purpose was to evaluate the island-effect on the plant community growing on the mounds/islands from two main aspects: (a) the influence of the area of the mounds on the species composition, diversity and dominance, and on the spatial distribution of the species on the surface of the mounds; (b) the differences between the plant communities of the mounds/islands and that of the surrounding cerrado, considered to be the 'mainland' source of the plants colonizing the mounds.

STUDY AREA

The area of campo de murundus studied is situated on the Fazenda São Pedro-Bandeira (15°30'S, 56°02'W, 190 m in altitutde), a cattle range located 14 km from Cuiabá, the capital of the state of Mato Grosso, central-western Brazil (see map in Oliveira-Filho 1992). The ranch extends over a typical area of the Baixada Cuiabana, a low plain with broad interfluves where the predominant

bedrock is a Pre-Cambrian phyllite. The climate is classified as Köppen's 'Savanna Subtype' (Aw), with high temperatures all year (annual mean of 25.6°C) and a rainy summer (October–May) and a dry winter (April–September): the mean annual rainfall of 1421 mm is concentrated (95%) during the period October–May. The predominant vegetation formation of the region is the cerrado (savanna) with its characteristic wide physiognomic variations, from an open scrub to a dense woodland (Oliveira-Filho & Martins 1991). Forests occur only as galleries along the watercourses and grasslands are found on rocky and/or poorly drained sites (Oliveira-Filho *et al.* 1989, 1990).

The campo de murundus and the surrounding cerrado lie at the top of a broad interfluve ($\pm$ 1.5 km wide). The campo, with an area of 5.065 ha, is on a flat sedimentary depression which forms a temporary shallow lake during the rainy season, when the low ridges around the perimeter of the field dam the water within. The seasonal floods cover the whole campo area with water to a depth of about 10 cm leaving the earthmounds as islands of drier soils.

The elevated areas around the campo de murundus are characterized by a thick superficial layer of quartzitic pebbles and are covered by cerrado with the physiognomy of a dense scrub of shrubs and trees and a sparse cover of subshrubs and herbs growing over the stony pavement (cerrado *sensu stricto* of Goodland (1971)). The area in the campo de murundus that is actually liable to be covered with water is a flat surface composed of alluvial sediments eroded from the surrounding elevated areas. It is entirely covered by a short-grass vegetation which is able to survive the floods.

The murundus of the study area are semi-elliptical earthmounds, with diameters ranging from 0.2 to 22.0 m and heights ranging from 0.1 to 1.1 m, which occupy 6.4% of the area of the campo de murundus. The 445 smaller mounds (< 0.8 m diameter) are found mainly in clumps and they are actually small termite nests built by *Armitermes euamignathus* Silvestri directly over the inundatable surface of the campo. The 80 larger mounds (> 0.8 m diameter) are regularly spaced and they are colonized by termites of the species *Cornitermes snyderi* Emerson and *Cornitermes bequaerti* Emerson which build large nests on the summit of the earthmounds. The soils of the earthmounds and termite nests have a finer texture, lower pH and higher amounts of mineral nutrients than those of the surrounding cerrado and of the seasonally inundated area. The vegetation growing on these mounds consists of cerrado plants with a wide physiognomic variation according to the size of the earthmounds, varying from tufts of subshrubs, on the smaller mounds; to a thick scrub, on the medium-sized mounds; and a dense forest, on the larger ones. More detailed descriptions of the geomorphology, soils, termite nests, vegetation physiognomy and authorities for plant names are given in Oliveira-Filho & Martins (1991).

METHODS

All earthmounds occurring in the campo de murundus were surveyed for their vegetation. Since most mounds occur in clumps, the survey units were the 'sets

of mounds'. Individual mounds were considered to be members of a set if the distances to nearest mounds were less than 2 m. Grouping the mounds in sets meant that the smaller ones (< 0.8 m diameter) were surveyed mainly in groups of one to five mounds (like 'archipelagos of islets') while the larger mounds (> 0.8 m diameter) occurred in sets with only one large mound and with or without additional small mounds (like a 'main island' with a few islets around). The area of each set of mounds was calculated (see Oliveira-Filho 1992) and they were categorized into seven classes of area, as follows: a: $0.05–0.50\,m^2$ (106 sets, $21.6\,m^2$ in total area); b: $0.51–2.00\,m^2$ (39, $38.2\,m^2$); c: $2.01–10.0\,m^2$ (21, $103.4\,m^2$); d: $10.1–35.0\,m^2$ (17, $361.4\,m^2$); e: $35.1–60.0\,m^2$ (14, $615.6\,m^2$); f: $60.1–100.0\,m^2$ (11, $855.8\,m^2$); and g: $100.1–300.0\,m^2$ (7, $1265.9\,m^2$).

Classes a, b and c were grouped in a single class abc for convenience in some calculations. The earthmounds of classes d, e, f and g were divided into concentric rings corresponding to classes of distance from the margin of the mounds. These distances corresponded to the diameters that limit the classes of mound area. Thus, the class g had four rings and the summit defined by the following distances from the margin: ring 1: 0–1.78 m; ring 2: 1.78–3.33 m; ring 3: 3.33–4.37 m; ring 4: 4.37–5.64 m; summit: 5.64–9.77 m. The class f had rings 1, 2 and 3, and the summit at 4.37–5.64 m; the class e had rings 1, and 2, and the summit at 3.33–4.37 m; the class d had ring 1 and the summit at 1.78–3.33 m; the class abc had only the summit at less than 1.78 m. Small mounds around a large mound were included as part of its ring 1. The classes of area and the rings were used to describe the distribution of the plant community acording to mound size and to topographic belts on the mounds.

The vegetation of each set of mounds was surveyed in two separate strata, hereafter called 'tall plants' and 'low plants'. The tall plants comprised the trees and shrubs, defined by more than 9 cm circumference at the base of the stem. The remaining plants, comprising subshrubs, herbs, climbers, acaulescent palms, bromeliads and seedlings, were all classified as low plants. According to this criterion some species could be sampled both as a small or as a tall plant, depending on their diameter.

The circumference at the base of the stem and the name of the species were recorded for each individual tall plant. The following parameters were calculated for each species in each class of mound area: density per unit area, relative density, basal area per unit area and relative dominance (relative basal area) (Matteucci & Colma 1982). The location of the individuals within the concentric rings of the mound was also recorded for a subsample of six species chosen by their higher values of total basal area. The basal area per unit was calculated for these species in each concentric ring of each class of mound area.

The low plants were surveyed by their percentage cover, which was estimated for each species on the surface of the mounds following the scores of Tüxen & Ellenberg (1937):

magnitude	percentage cover	average percentage cover
+	< 1%	0.1%
1	1–10%	5.0%
2	10–25%	17.5%
3	25–50%	37.5%
4	50–75%	62.5%
5	75–100%	87.5%

The cover value of Tüxen & Ellenberg (1937) was calculated for each species in each class of mound area:

$$\text{cover value} = \frac{\text{sum of the values of average percentage cover} \times 100}{\text{number of inventories}}$$

The percentage cover was also estimated in each concentric ring of the mounds for a subsample of six species. These were chosen among those reaching higher values of percentage cover in any particular section of the sequence of classes of mound area. The cover value was calculated for these species in each ring of each class of mound area.

Nine typical sets of mounds were chosen and drawings made of their vertical projections in order to illustrate the spatial arrangement of the plants on the earthmounds of all size classes.

The cerrado that surrounds the campo de murundus was also surveyed for its tall plants which were sampled using the Point-Centred Quarter method (PCQ), as described by Mueller-Dombois & Ellenberg (1974). The points were distributed in four concentric Arcs – I, II, III and IV – at the distances of 10, 20, 30 and 40 m, respectively, from the margin of the cerrado where it is suddenly replaced by the campo de murundus. Each arc had 35 points spaced 10 m apart. The species, the circumference at the base of the stem and the point-plant distance were recorded for each nearest individual in each point quarter. The same parameters obtained for the tall plants of the mounds were also calculated for each species in each arc of points.

The number of species and the area of the set of mounds were used for linear regressions of species number on area which were carried out with two models. The first one was the power model, or log-log model, $S = C(A^z)$, where S is the number of species growing on an island of area A; C and z are fitted constants. This model was considered by Preston (1962) and MacArthur & Wilson (1963, 1967) as the best to describe species-area relationships in island ecology and it is very widespread in the literature (Connor & McCoy 1979). The second model used was the exponential, or linear-log, $S = C + z(\log A)$. This model has provided the best fit when applied to many studies on plant communities in ecological islands (Buckley 1982, Møller & Rørdan 1985, Nilsson & Nilsson 1978, Rydin & Borgegård 1988).

The Shannon-Wiener diversity index (H′) and the Pielou evenness (J′) (Brower & Zár 1984) were calculated for the species of low and tall plants in each class of mound area and for each concentric arc of the surrounding cerrado. The abundance values used to calculate H′ were the number of individuals for the tall plants, and the average percentage cover for the low plants.

Ordinations by Detrended Correspondence Analyses (DECORANA) were carried out using a computer program based on Hill (1979). A first ordination processed the seven subcommunities defined by the classes of mound area and their species of tall and low plants. A second DECORANA processed the above subcommunities plus the four subcommunities defined by the concentric sample arcs of the surrounding cerrado, considering only the species of tall plants of both areas. Less abundant species were eliminated from the initial matrices of both ordinations. In the first ordination, the abundance values used for the species of low plants in the sample by species matrix were the cover values, while those used for the species of tall plants in both ordinations were the relative basal areas. The cover values were transformed into relative values in order to use only relative abundances on the ordination procedures. Hierarchical classifications by clustering were also carried out with the same matrices used in the DECORANA. The coefficient of similarity used was the Squared Euclidean Distance (Gauch 1982) and the clustering followed the technique of Average Grouping (Everitt 1980). Although using different sampling methods for the vegetation of the mounds and of the surrounding cerrado, the high sampling intensity certainly attenuates the potential problems of comparing these two communities.

RESULTS

The complete lists of species registered in the surveys are given in Tables 1, 2 and 3. The cover values of the species of low plants in each class of earthmound area are given in Table 1, while Table 2 gives the density ha^{-1} and the basal area ha^{-1} of the species of tall plants. These same data are given in Table 3 for the species of tall plants in each of the four concentric sample arcs of the surrounding cerrado. There are some doubts among those working on the vegetation of Mato Grosso regarding the identity of the species of *Tabebuia*. Thus it is worth noting that the species referred to in the present paper as *T. aurea* and *T. caraiba* correspond, respectively, to *T. serratifolia* (Vahl) Nichols and *T. aurea* (Manso) Benth. & Hook. in the recent revision by Gentry (1992).

The community of low plants in the smaller earthmounds (Classes a, b and c) was dominated by a single species, *Annona pygmaea*, which presented a cover value ranging from 7740 to 8750. The next species *Waltheria* sp. had less than 500 of cover value. As the area of the mounds increased, the importance of *Annona pygmaea* decreased while new species were being added to the community. The cover value of most species increased towards a peak at the Classes f or g, as with *Bromelia balansae, Annona dioica, Matayba guianensis, Allagoptera leucocalyx,*

Table 1. Species of low plants (< 9 cm circumference at the base of the stem) surveyed in the cerrado vegetation of the murundus with their cover values in each of the seven classes of mound area (see pp. 468–469). Authorities for the species and their families can be found in Oliveira-Filho & Martins (1991).

Classes of mound area:	Cover value							
	a	b	c	d	e	f	g	Total
Species:								
Bromelia balansae	–	80	190	570	1100	760	2690	1520
Annona pygmaea	8750	8330	740	2170	500	500	500	1060
Allagoptera leucocalyx	10	20	90	350	690	1000	910	790
Vernonia brasiliana	40	100	140	420	460	570	660	550
Annona dioica	–	20	–	–	240	960	640	550
Copaifera martii	–	–	180	580	730	240	250	370
Matayba guianensis	–	–	30	120	190	430	220	250
Simaba trichilioides	–	–	230	220	530	300	90	250
Arrabidaea corallina	–	–	60	100	260	140	360	240
Myrcia suffruticosa	–	–	–	220	270	240	230	220
Waltheria sp.	300	500	260	150	110	90	90	110
Psidium multiflorum	–	–	30	140	90	140	110	110
Byrsonima dealbata	–	–	–	–	–	330	–	90
Abuta selloana	–	–	–	–	30	140	50	60
Smilax sp.	–	–	70	100	–	130	–	50
Diospyros coccolobifolia	–	–	–	–	–	40	70	40
Cordia insignis	–	–	–	–	60	–	50	30
Bauhinia rufa	–	–	–	–	–	–	70	30
Serjania sp.	–	–	–	–	–	–	70	30
Byrsonima subterranea	–	–	–	–	–	50	–	10
Dipteryx alata	–	–	–	–	50	–	–	10
Curatella americana L.	–	450	100	–	–	–	–	10
Strychnos pseudo-quina	–	–	–	–	40	–	–	10
Anacardium humile	–	–	30	20	–	–	–	10
Alibertia edulis	–	–	40	–	–	–	–	10
Casearia sylvestris	–	–	30	–	–	–	–	10
Tocoyena formosa	–	–	20	–	–	–	–	10
Erythroxylum suberosum	–	–	10	–	–	–	–	10
number of species:	4	7	17	13	16	17	17	28
H':	0.2	0.5	0.8	2.0	2.4	2.5	2.1	2.4
J':	0.1	0.3	0.3	0.8	0.9	0.9	0.8	0.7

H': = Shannon-Wiener diversity index
J': = Pielou evenness.

Vernonia brasiliana and *Arrabidaea corallina*. Other species, such as *Copaifera martii*, *Simaba trichilioides* and *Myrcia suffruticosa* showed their peaks at the intermediate class e.

The community structure among the tall plants also varied with mound area. *Curatella americana* was the most important species in all classes of mound area, although its relative importance decreased with increasing mound area. This decrease in importance with increasing mound size was also observed for *Simarouba versicolor* and *Matayba guianensis*. Some species, such as *Hymenaea stigonocarpa*, *Eugenia aurata* and *Astronium fraxinifolium*, presented their occurrence peak in the classes of larger mounds (f and g) while others, such as *Dipteryx alata*, *Tabebuia aurea*, *Andira cuyabensis*, *Alibertia edulis* and *Erythroxylum suberosum*, had their peaks at the classes of medium sized mounds (d and e).

Table 2. Species of tall plants (> 9 cm circumference at the base of the stem) surveyed in the cerrado vegetation of the murundus with their density ha^{-1} (D) and basal area ha^{-1} (BA) in each class of mound area (see page 468). The species are arranged in descending order of density. Authorities for the species and their families can be found in Oliveira-Filho & Martins (1991).

Classes of mound area		abc	d	e	f	g	Total
Species:							
Curatella americana	D:	2452	1356	1721	1227	758	1234
	BA:	44.93	14.80	15.66	12.66	6.94	13.07
Alibertia edulis	D:	245	387	374	222	174	255
	BA:	1.65	2.30	1.67	1.57	0.98	1.47
Dipteryx alata	D:	61	194	162	140	126	143
	BA:	0.05	6.68	6.84	6.26	6.75	6.40
Andira cuyabensis	D:	184	304	114	117	95	137
	BA:	8.52	0.72	1.49	2.42	1.30	1.57
Tabebuia aurea	D:	–	221	227	82	47	109
	BA:	–	2.61	2.84	1.27	0.79	1.49
Eugenia aurata	D:	–	138	146	175	32	103
	BA:	–	0.67	0.52	0.59	0.23	0.42
Erythroxylum suberosum	D:	123	249	130	58	40	90
	BA:	0.17	1.46	0.33	0.13	0.20	0.35
Pseudobombax longiflorum	D:	245	28	16	129	47	72
	BA:	0.61	0.82	0.03	0.32	0.07	0.24
Matayba guianensis	D:	184	110	65	23	24	53
	BA:	0.24	0.11	0.12	0.04	0.02	0.07
Tabebuia caraiba	D:	184	–	–	47	63	40
	BA:	1.72	–	–	0.22	0.37	0.29
Hymenaea stigonocarpa	D:	–	–	65	70	40	47
	BA:	–	–	2.01	4.26	2.28	2.42
Simarouba versicolor	D:	306	83	65	23	8	47
	BA:	3.69	1.66	0.57	0.81	0.01	0.70
Astronium fraxinifolium	D:	–	–	–	23	47	31
	BA:	–	–	–	0.10	0.35	0.16
Byrsonima pachyphylla	D:	61	28	49	35	8	28
	BA:	0.10	0.43	0.25	0.06	0.13	0.17
Vatairea macrocarpa	D:	123	–	49	35	–	25
	BA:	3.33	–	0.98	1.86	–	0.85
Sclerolobium aureum	D:	–	28	16	58	8	25
	BA:	–	0.29	0.05	0.37	0.01	0.14
Abuta selloana	D:	–	28	16	47	16	25
	BA:	–	0.09	0.30	0.05	0.31	0.21
Brosimum gaudichaudii	D:	–	28	32	47	8	25
	BA:	–	0.03	0.18	0.09	0.04	0.08
Cecropia pachystachya	D:	–	–	32	–	40	22
	BA:	–	–	1.09	–	0.59	0.44
Campomanesia eugenioides	D:	–	–	114	–	–	22
	BA:	–	–	0.23	–	–	0.04
Bowdichia major	D:	–	–	81	–	8	19
	BA:	–	–	0.25	–	0.10	0.09
Jacaranda cuspidifolia	D:	61	–	–	23	16	16
	BA:	1.48	–	–	0.43	0.66	0.45
Copaifera martii	D:	–	–	16	35	8	16
	BA:	–	–	0.65	0.05	0.02	0.15
Cybistax antisyphilitica	D:	–	83	–	–	16	16
	BA:	–	0.17	–	–	0.12	0.07
Pouteria ramiflora	D:	–	55	–	23	–	12
	BA:	–	0.75	–	0.16	–	0.13
Diospyros coccolobifolia	D:	–	28	16	12	8	12
	BA:	–	0.49	0.03	0.10	0.06	0.11
Casearia sylvestris	D:	–	–	–	12	24	12
	BA:	–	–	–	0.09	0.12	0.07

(cont.)

Table 2 (cont.).

Classes of mound area		abc	d	e	f	g	Total
Heteropterys byrsonimifolia	D:	–	28	32	–	–	9
	BA:	–	0.07	0.34	–	–	0.07
Qualea parviflora	D:	–	–	–	12	16	9
	BA:	–	–	–	0.11	0.03	0.04
Erythroxylum citrifolium	D:	–	28	–	12	–	6
	BA:	–	0.02	–	0.01	–	0.01
Simaba trichilioides	D:	–	28	–	12	–	6
	BA:	–	0.02	–	0.01	–	0.01
Bauhinia bongardi	D:	–	–	–	–	16	6
	BA:	–	–	–	–	0.02	0.01
Zanthoxylum cinereum	D:	–	–	–	–	8	3
	BA:	–	–	–	–	0.24	0.10
Myrcia formosiana	D:	–	28	–	–	–	3
	BA:	–	0.23	–	–	–	0.03
Himatanthus obovatus	D:	–	–	–	–	8	3
	BA:	–	–	–	–	0.03	0.01
Magonia pubescens	D:	–	–	–	–	8	3
	BA:	–	–	–	–	0.03	0.01
Rudgea viburnioides	D:	61	–	–	–	–	3
	BA:	0.20	–	–	–	–	0.01
Kielmeyera coriacea	D:	–	–	–	–	8	3
	BA:	–	–	–	–	0.02	0.01
Vernonia brasiliana	D:	61	–	–	–	–	3
	BA:	0.14	–	–	–	–	0.01
Ouratea hexasperma	D:	–	–	16	–	–	3
	BA:	–	–	0.03	–	–	0.01
Myrcia uberavensis	D:	–	–	16	–	–	3
	BA:	–	–	0.02	–	–	0.01
Cardiopetalum calophyllum	D:	–	–	16	–	–	3
	BA:	–	–	0.02	–	–	0.01
Connarus suberosus	D:	–	28	–	–	–	3
	BA:	–	0.02	–	–	–	0.01
Annona pygmaea	D:	61	–	–	–	–	3
	BA:	0.05	–	–	–	–	0.01
Tocoyena formosa	D:	–	–	–	12	–	3
	BA:	–	–	–	0.01	–	0.01
Number of individuals:		74	126	221	232	218	871
Density (ha^{-1}):		4535	3486	3590	2710	1722	2713
Total basal area (m^2):		0.97	1.24	2.25	2.91	2.89	10.26
Total basal area (m^2 ha^{-1}):		59.20	34.43	36.48	34.03	22.82	31.96
Number of species:		15	22	25	27	30	45
H':		1.82	2.25	2.12	2.26	2.30	2.36
J':		0.67	0.73	0.66	0.69	0.68	0.62

H': = Shannon-Wiener diversity index
J': = Pielou evenness.

In the surrounding cerrado, the community of tall plants also showed variations in structure with increasing distance from the campo de murundus (Table 3). It was observed that *Dipteryx alata* and *Curatella americana*, which are also abundant on the mounds, are more common at the concentric Arcs I (margin of the cerrado) and II (subsequent arc), respectively. The species of Vochysiaceae, *Vochysia rufa*, *Salvertia convallariodora* and *Qualea parviflora*, which are virtually

Table 3. Species of tall plants (> 9 cm circumference at the base of the stem) surveyed by Point Centred Quarter method (PCQ) in the cerrado vegetation which surrounds the campo de murundus with their density ha^{-1} (D) and basal area ha^{-1} (BA) in each concentric arc of sample dots (see page 469). The species are arranged in descending order of density. Authorities for the species and their families can be found in Oliveira-Filho & Martins (1992).

Concentric sample arcs:		I	II	III	IV	Total
Species:						
Qualea parviflora	D:	135	84	197	176	146
	BA:	2.25	1.50	1.84	3.19	2.19
Curatella americana	D:	95	129	91	63	96
	BA:	2.02	3.12	1.67	0.89	1.96
Salvertia convallariodora	D:	71	45	151	85	87
	BA:	1.38	0.72	2.04	0.77	1.20
Myrcia uberavensis	D:	63	84	76	77	76
	BA:	0.42	0.73	0.46	0.53	0.55
Vochysia rufa	D:	16	26	61	92	49
	BA:	0.31	0.33	1.93	2.11	1.16
Qualea grandiflora	D:	71	45	23	49	47
	BA:	1.32	0.72	0.23	0.53	0.69
Pouteria ramiflora	D:	8	39	45	42	34
	BA:	0.18	0.92	0.43	0.73	0.59
Salacia crassifolia	D:	32	45	8	35	31
	BA:	0.29	0.46	0.09	0.63	0.38
Davilla elliptica	D:	40	19	38	28	31
	BA:	0.22	0.17	0.25	0.21	0.21
Dipteryx alata	D:	79	13	7	–	23
	BA:	4.00	0.17	0.51	–	1.08
Bowdichia major	D:	40	19	15	7	20
	BA:	0.96	0.12	0.23	0.18	0.35
Connarus suberosus	D:	24	19	45	21	27
	BA:	0.11	0.04	0.12	0.13	0.10
Sclerolobium aureum	D:	24	19	15	28	22
	BA:	0.05	0.06	0.03	0.06	0.05
Tabebuia caraiba	D:	24	19	15	14	18
	BA:	0.29	0.17	0.31	0.24	0.25
Pseudobombax longiflorum	D:	16	19	8	21	16
	BA:	0.04	0.73	0.22	0.50	0.39
Andira cuyabensis	D:	16	19	8	21	16
	BA:	0.61	0.21	0.17	0.28	0.31
Diospyros coccolobifolia	D:	8	19	30	7	16
	BA:	0.0 1	0.07	0.07	0.02	0.22
Brosimum gaudichaudii	D:	40	19	8	–	16
	BA:	0.13	0.07	0.04	–	0.06
Byrsonima coccolobifolia	D:	16	6	23	14	14
	BA:	0.11	0.08	0.61	0.11	0.22
Byrsonima pachyphylla	D:	16	26	8	7	14
	BA:	0.09	0.49	0.05	0.03	0.18
Erythroxylum suberosum	D:	24	13	–	21	14
	BA:	0.25	0.07	–	0.15	0.11
Simarouba versicolor	D:	8	13	8	21	13
	BA:	0.26	0.11	0.30	0.17	0.21
Astronium fraxinifolium	D:	8	–	23	14	11
	BA:	0.33	–	–	0.04	0.16
Dimorphandra mollis	D:	–	19	8	14	11
	BA:	–	0.10	0.07	0.35	0.13

Table 3 (cont.). .

Concentric sample arcs:		I	II	III	IV	Total
Tabebuia ochracea	D:	8	13	15	7	11
	BA:	0.07	0.06	0.20	0.10	0.11
Tabebuia aurea	D:	32	6	–	7	11
	BA:	0.33	0.01	–	0.05	0.09
Ouratea spectabilis	D:	8	–	15	14	9
	BA:	0.04	–	0.13	0.15	0.08
Annona coriacea	D:	24	6	–	7	9
	BA:	0.05	0.03	–	0.01	0.02
Hymenaea stigonocarpa	D:	8	13	–	7	7
	BA:	0.28	0.69	–	0.01	0.26
Vatairea macrocarpa	D:	16	6	–	7	7
	BA:	1.18	0.01	–	0.33	0.36
Himatanthus obovata	D:	8	–	15	7	7
	AB:	0.10	–	0.17	0.02	0.07
Lafoensia pacari	D:	–	6	8	14	7
	BA:	–	0.04	0.02	0.12	0.05
Agonandra brasiliensis	D:	16	13	–	–	7
	BA:	0.06	0.10	–	–	0.04
Magonia pubescens	D:	–	6	15	–	5
	BA:	–	0.19	0.18	–	0.10
Ouratea hexasperma	D:	8	–	8	7	5
	BA:	0.04	–	0.14	0.07	0.06
Ferdinandusa elliptica	D:	8	6	–	7	5
	BA:	0.04	0.02	–	0.15	0.05
Matayba guianensis	D:	8	6	8	–	5
	BA:	0.05	0.05	0.02	–	0.03
Strychnos pseudo-quina	D:	–	13	–	–	4
	BA:	–	0.34	–	–	0.10
Dilodendron bipinnatum	D:	–	–	15	–	4
	BA:	–	–	0.19	–	0.05
Eriotheca gracilipes	D:	8	6	–	–	4
	BA:	0.12	0.03	–	–	0.04
Pseudobombax tomentosum	D:	8	–	8	–	4
	BA:	0.03	–	0.07	–	0.02
Myrcia pallens	D:	8	6	–	–	4
	BA:	0.04	0.03	–	–	0.02
Kielmeyera coriacea	D:	8	–	8	–	4
	BA:	0.02	–	0.03	–	0.01
Diptychandra aurantiaca	D:	8	6	–	–	4
	BA:	0.03	0.01	–	–	0.01
Kielmeyera rubriflora	D:	–	6	–	7	4
	BA:	–	0.01	–	0.02	0.09
Acrocomia aculeata	D:	8	–	–	–	2
	BA:	0.27	–	–	–	0.06
Dalbergia myscolobium	D:	–	–	–	7	2
	BA:	–	–	–	0.21	0.05
Jacaranda cuspidifolia	D:	–	–	–	7	2
	BA:	–	–	–	0.16	0.04
Platypodium elegans	D:	8	–	–	–	2
	BA:	0.17	–	–	–	0.04
Aspidosperma macrocarpon	D:	8	–	–	–	2
	BA:	0.14	–	–	–	0.03
Alibertia edulis	D:	–	–	8	–	2
	BA:	–	–	0.08	–	0.02
Hancornia speciosa	D:	–	6	–	–	2
	BA:	–	0.06	–	–	0.02

Table 3 (cont.).

Concentric sample arcs:		I	II	III	IV	Total
Eugenia aurata	D:	–	6	–	–	2
	BA:	–	0.05	–	–	0.01
Stryphnodendron obovatum	D:	–	–	8	–	2
	BA:	–	–	0.05	–	0.01
Hirtella gracilipes	D:	–	–	8	–	2
	BA:	–	–	0.04	–	0.01
Rudgea viburnioides	D:	–	–	–	7	2
	BA:	–	–	–	0.04	0.01
Coccoloba mollis	D:	–	–	–	7	2
	BA:	–	–	–	0.03	0.01
Eugenia uniflora	D:	–	–	8	–	2
	BA:	–	–	0.03	–	0.01
Neea theifera	D:	–	–	8	–	2
	BA:	–	–	0.03	–	0.006
Coussarea hydrangeaefolia	D:	8	–	–	–	2
	BA:	0.02	–	–	–	0.005
Cardiopetalum calophyllum	D:	8	–	–	–	2
	BA:	0.02	–	–	–	0.005
Cybistax antisyphilitica	D:	8	–	–	–	2
	BA:	0.02	–	–	–	0.005
Acosmium dasycarpum	D:	–	–	–	7	2
	BA:	–	–	–	0.01	0.003
Casearia sylvestris	D:	8	–	–	–	2
	BA:	0.01	–	–	–	0.002
Tocoyena formosa	D:	–	6	–	–	2
	BA:	–	0.01	–	–	0.001
Number of individuals:		140	140	140	140	560
Density (ha^{-1}):		1156	938	1100	1024	1050
Total basal area (m^2):		19.53	13.40	13.85	13.84	15.03
Basal area (m^2 ha^{-1}):		2.365	1.999	1.762	1.892	8.018
Number of species:		46	41	38	38	65
H':		3.38	3.28	3.01	3.12	3.40
J':		0.88	0.88	0.83	0.86	0.81

H' = Shannon-Wiener diversity index
J' = Pielou evenness.

absent in the mounds, occurred more frequently at the Arcs III and IV of the surrounding cerrado.

Regressions of number of plant species on mound area yielded the following equations: $S = 0.943 \ (A^{0.366})$ (power model or log-log) and $S = 3.987 + 1.887(\log A)$ (exponential or linear-log model). For predictive purposes, the regression equation with the power model seems to be preferable because it yielded the higher coefficient of determination; $r^2 = 0.89$, against $r^2 = 0.76$, provided by the exponential model. Figure 1a illustrates the line fitted by linear regression with the power model.

The Tables 1, 2 and 3 also give, at the foot, the total number of species (S), the Shannon-Wiener diversity index (H') and the Pielou evenness (J') for each subcommunity surveyed in the study area. The total number of species as well as the number of species of tall and low plants surveyed in each class of mound
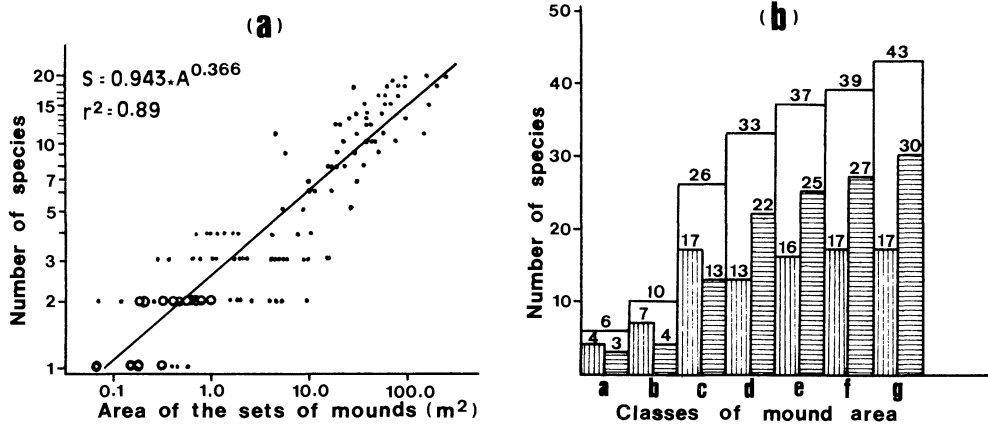
Figure 1. Number of plant species occurring on the mounds: (a) relationship between total number of species and area of the set of earthmounds; S = number of plant species, A = area of the set of mounds (open dots represent coincident coordinates; note log scales); (b) number of species of low (vertical hatching) and tall plants (horizontal hatching) and total number of species (empty large bar) in each class of mound area.

area is illustrated by Figure 1b. Both H' and J' increased for the species of low plants from very low values, in the smaller mounds, to the highest values reached at the Class f of mound area, decreasing a little at the last Class, g (Table 1). However, the number of species of low plants did not vary much in the classes of larger mounds, from e to g (Figure 1b). In the case of the tall plants, the classes of smaller mounds (a, b and c) presented the lowest and the highest values of H' and J', respectively, while the remaining classes showed little variation for these indices (Table 2) in spite of the increase in the number of species (Figure 1b). This indicates that, although it is less diverse, the community of tall plants on the smaller mounds had a lower concentration of relative abundances in fewer species (lower ecological dominance). The species diversity in the surrounding cerrado, did not vary significantly between the concentric sample arcs (Table 3).

The Figures 2 and 3 show some profiles of the vegetation for nine chosen sets of mounds in order to illustrate the changes in species composition and spatial distribution along the gradient of mound size, all classes of mound being represented by one drawing. The spatial distribution of 12 important species of low and tall plants on the mound's surface according to mound size and to topographic belts on the mounds is shown by Figure 4.

The classes with the smallest mounds (a and b) were normally represented by sets of very small mounds (dead nests of *Armitermes euamignathus*) which were predominantly covered by the subshrub *Annona pygmaea*, associated with the less abundant *Waltheria* sp. However, some small shrubs of *Curatella americana* and *Vernonia brasiliana* could grow in the larger mounds of these classes (Figure 2a,b). The Class c of mound area (Figure 2c) was represented mainly by single earthmounds formed from the coalescence of smaller mounds as a result of soil accumulation by termite activity (*Cornitermes* spp.). The vegetation cover was almost entirely composed of tufts of *Annona pygmaea* and shrubs of *Curatella*
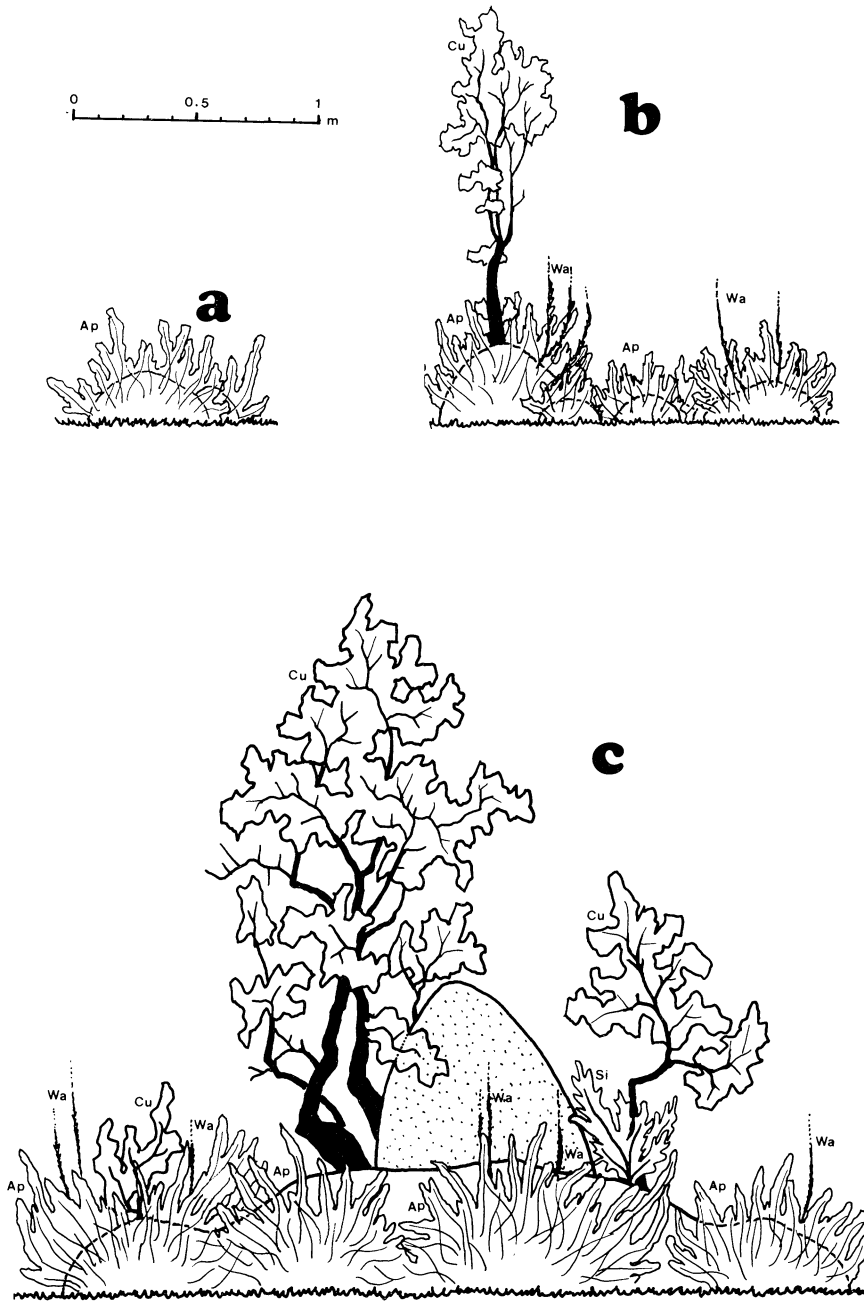
Figure 2.   Profiles of three sets of mounds showing the distribution of the plant species on the surface of the mounds of area classes a, b and c. Plant species: Ap – *Annona pygmaea*; Cu – *Curatella americana*; Si – *Simaba trichilioides*; Ve – *Vernonia brasiliana*; Wa – *Waltheria* sp.
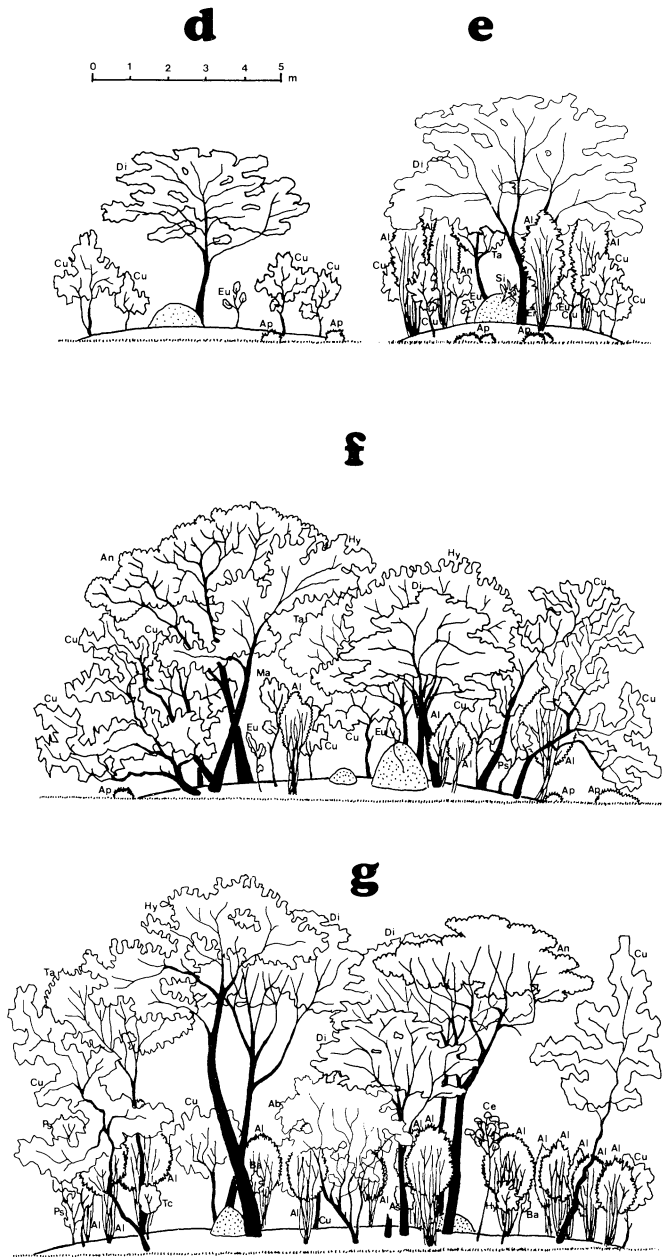
Figure 3. Profiles of four sets of mounds showing the distribution of the plant species on the surface of the mounds of area classes d, e, f and g. Plant species: Ab – *Abuta selloana;* Al – *Alibertia edulis*; An – *Andira cuyabensis*; Ap – *Annona pygmaea*; As – *Astronium fraxinifolium*; Ba – *Bauhinia bongardi*; Ce – *Cecropia pachystachya*; Cu – *Curatella americana*; Di – *Dipteryx alata*; Er – *Erythroxylum suberosum*; Eu – *Eugenia aurata*; Hy – *Hymenaea stigonocarpa*; Ma – *Matayba guianensis*; Ps – *Pseudobombax longiflorum*; Si – *Simaba trichilioides*; Ta – *Tabebuia aurea*; Tc – *Tabebuia caraiba*.
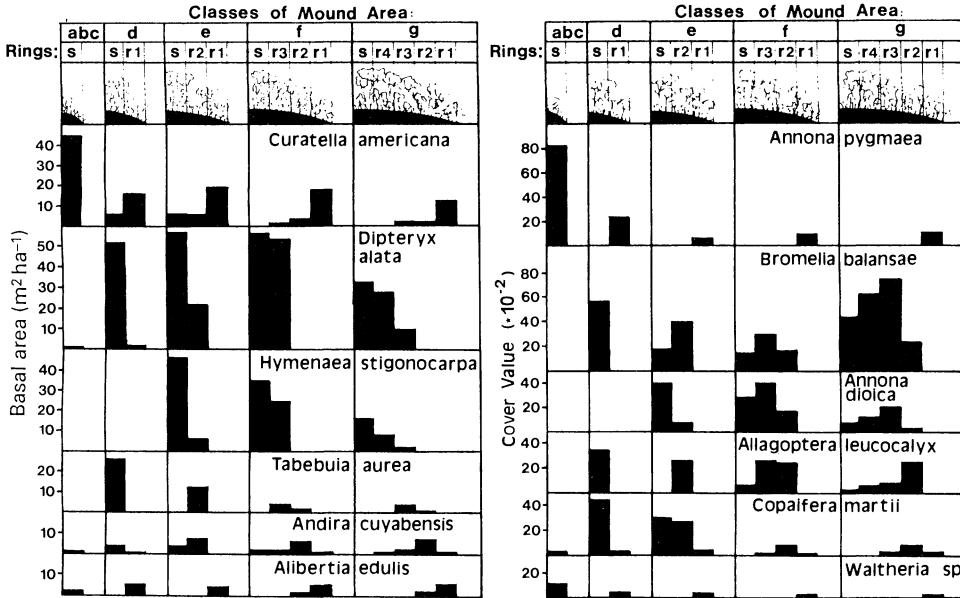
Figure 4.   Spatial distribution of six species of tall (left) and low plants (right) on the concentric topographic rings of each class of mound area. The summit of the mounds is represented by s and the successive rings by r1 to r4. The abundance of the tall plants is represented by their basal area ha^{-1} and the abundance of the low plants by their cover value (divided by 100).

americana. The dominance of these two species in the vegetation of the smaller mounds (Classes a, b and c) is also shown in Figure 4.

As the size of the mounds increased in Classes d, e, f and g (Figure 3), the occurrence of *Annona pygmaea* was first restricted to the margin of the mounds and then to the small mounds ('islets') around a main large mound. As shown by Figure 4, the surface of these larger mounds was covered by other species of low plants, such as *Allagoptera leucocalyx* (an acaulescent palm) and *Copaifera martii* (seedlings), that were more concentrated near the margins, and *Bromelia balansae* (a bromeliad) and *Annona dioica* (a subshrub), which were more concentrated between the margins and the summits.

The spatial disposition of the community of tall plants on the surface of the larger mounds (Classes d, e, f and g) was characterized by well defined associations corresponding to topographic belts. *Curatella americana* was found growing as a marginal belt of shrubs and trees together with the shrubs of *Alibertia edulis* (Figure 3). Some species of tall trees, such as *Dipteryx alata* and *Hymenaea stigonocarpa*, occurred mainly at the summit of the mounds, while other species of lower trees, such as *Tabebuia aurea* and *Andira cuyabensis*, occurred more often between the *Curatella*/*Alibertia* outer belt and the *Dipteryx*/*Hymenaea* centre (Figure 4).

The results of the ordination of subcommunities and species, together with respective cluster dendrograms, are shown in Figures 5 and 6. The ordination of the seven classes of mound area (Figure 5a) shows, on the first axis, the three larger classes all together and then a decreasing sequence according to mound
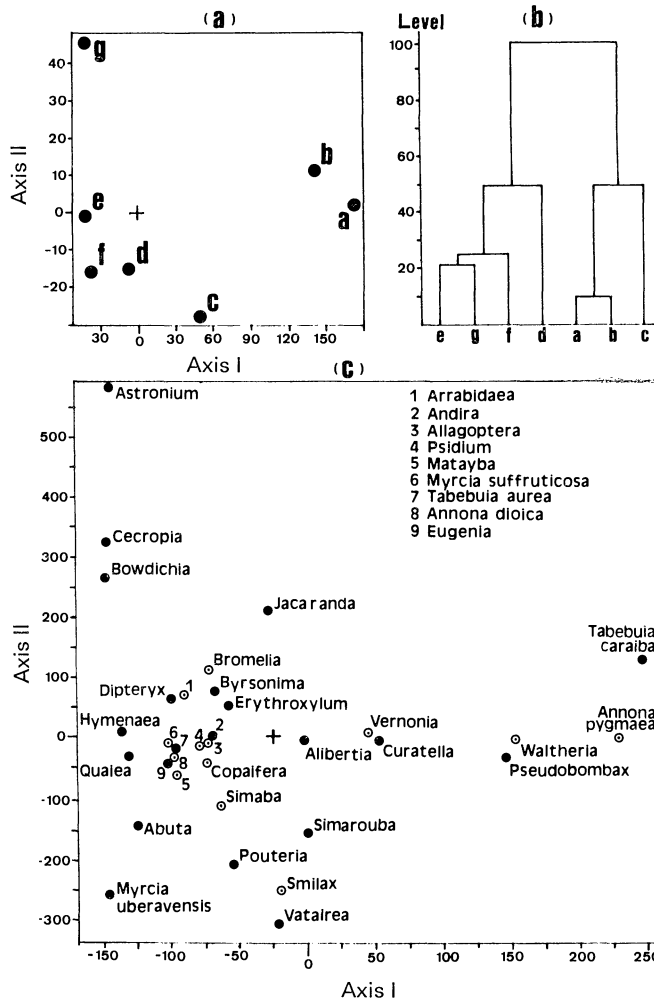
Figure 5. Results of multivariate analyses of seven subcommunities of the murundu cerrado, defined by the seven classes of mound area, and of their species of low and tall plants: (a) ordination by detrended correspondence analyses of the seven subcommunities in the first two ordination axes; (b) cluster dendrogram showing the hierarchical classification of the same subcommunities; (c) ordination by detrended correspondence analyses of 21 species of tall plants (black dot) and 13 species of low plants (ringed dots) in the two first ordination axes. The species are indicated by their genera, except when there are two species in the same genus.

size. These larger classes were best separated by the second ordination axis. Both the ordination and the dendrogram (Figure 5b) show the Classes a/b and e/f/g at the opposite ends of the gradient. The ordination of the species (Figure 5c) shows, at the right, a characteristic group of species of the smaller mounds: *Annona pygmaea*, *Waltheria* sp., *Tabebuia caraiba* and *Pseudobombax longiflorum*. Species characteristic of the larger mounds are found as a dense cloud of points at the centre left, consisting of *Hymenaea stigonocarpa*, *Dipteryx alata*, *Tabebuia aurea*, *Andira cuyabensis*, *Allagoptera leucocalyx*, *Bromelia balansae* and *Annona dioica*. Species almost exclusive to the largest mound Class (g), such as *Cecropia pachystachya*, *Astronium*
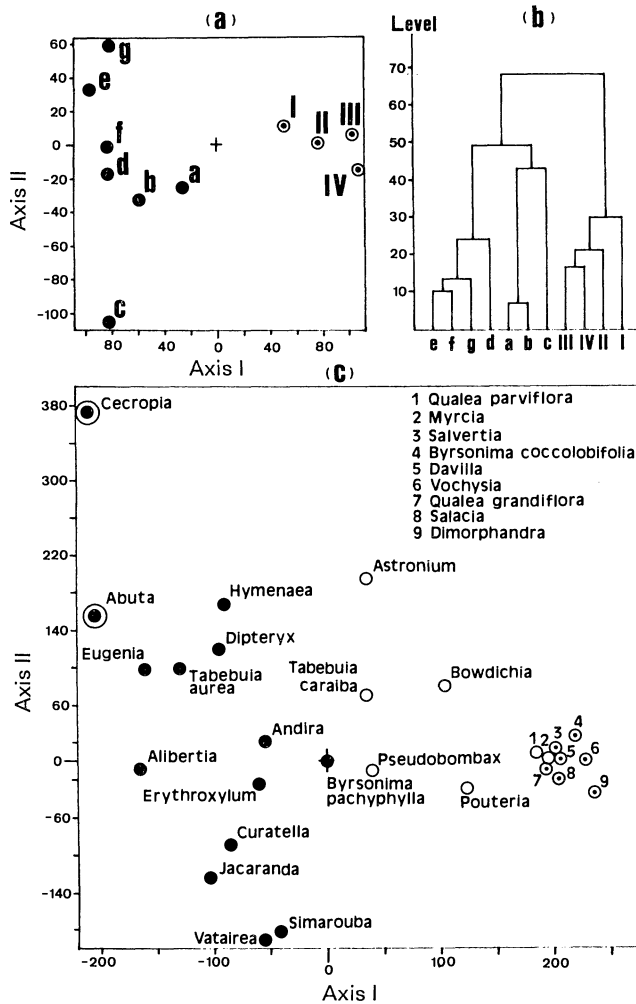
Figure 6.   Results of multivariate analyses of 11 subcommunities of cerrado, defined by the seven classes of mound area of the murundu cerrado (a to g) and by the four concentric sample lines of the surrounding cerrado (I to IV), and of their species of tall plants: (a) ordination by detrended correspondence analyses of the 11 subcommunities in the first two ordination axes; (b) cluster dendrogram showing the hierarchical classification of the same subcommunities; (c) ordination by detrended correspondence analyses of 28 species of tall plants in the first two ordination axes. The big ringed dots represent the species exclusive to the murundu cerrado; the black dots represent the species that are more abundant in the murundu cerrado; the open dots represent the species that are more common in the surrounding cerrado and the small ringed dots represent the species exclusive to the surrounding cerrado. The species are indicated by their genera, except when there are two species in the same genus.

fraxinifolium and *Bowdichia major*, are shown at the top left. At the centre of the first axis are found the species which are common throughout the gradient, such as *Curatella americana*, *Vernonia brasiliana*, *Alibertia edulis* and *Simarouba versicolor*.

The seven classes of mound area and the four concentric sample arcs of the surrounding cerrado were separated as two discrete communities both by the ordination (Figure 6a) and by the cluster dendrogram (Figure 6b). The points

corresponding to the surrounding cerrado appear at the right in the first ordination axis, with the Arcs III and IV (the more distant from the margin) at the extreme right. The points corresponding to the murundu cerrado are found at the left with the second axis separating the classes of mound area from one another. The ordination of the species (only tall plants were considered) (Figure 6c) shows at the extreme right a very dense cloud of points corresponding to exclusive species of the surrounding cerrado, such as *Vochysia rufa, Salvertia convallariodora, Qualea grandiflora, Davilla elliptica, Salacia crassifolia* and *Dimorphandra mollis*. This group is followed to the left by species common to both communities, but more abundant in the surrounding cerrado, such as *Pouteria ramiflora, Bowdichia major, Pseudobombax longiflorum, Astronium fraxinifolium* and *Tabebuia caraiba*. At the left, are found the species that are more abundant in the murundu cerrado, such as *Curatella americana, Dipteryx alata, Hymenaea stigonocarpa, Tabebuia aurea, Alibertia edulis, Andira cuyabensis* and *Eugenia aurata*. The axis ends with the two species exclusive to the murundu cerrado: *Abuta selloana* and *Cecropia pachystachya*.

DISCUSSION

The particular type of vegetation that covers the earthmounds of the campo de murundus results from a well known characteristic of most species of the cerrado formation: they do not tolerate water-logging, even for short periods (Eiten 1972). The maximum level reached by floods or by outcropping water table commonly defines sharp boundaries to the distribution of cerrado vegetation as a whole, which is suddenly replaced under these conditions by marshy grasslands or gallery forests (Furley & Ratter 1988, Ratter *et al.* 1973). However, the cerrado species are not equally intolerant of water-logging, and particular subcommunities are normally found in those areas where the cerrado meets those hydrophilous formations under conditions of seasonally superficial water table (Oliveira-Filho *et al.* 1989). This is what probably occurs in the marginal areas of the cerrado surrounding the campo de murundus where they indicate the boundaries of the inundatable surface of the campo de murundus and this certainly explains the higher similarity between this subcommunity and the murundu cerrado.

When the campo de murundus is flooded, the earthmounds are not covered by water, but, as observed in many bore holes, the water table in the mounds is normally found only a few centimeters below the flooding level in the campo. Thus, the cerrado community occurring on the mounds is certainly composed of less intolerant species. The vegetation surveyed on those mounds showed high similarity in floristic composition, especially of the ecological dominants, to other cerrado communities found on murundus of seasonally flooded areas of Central Brazil (Cunha *et al.* 1983, Ratter 1987, Ratter *et al.* 1973, 1988).

The ecological dominant of the murundu cerrado, *Curatella americana*, is, within the cerrado flora, one of the most tolerant species of seasonal soil saturation. In the state of Mato Grosso, Ratter *et al.* (1973) and Oliveira-Filho *et al.* (1989) found *Curatella americana* in marginal areas of cerrado where the water table

reaches its highest level, below which the cerrado was replaced by valley-side marshes. This species is also dominant in the murundus of the Pantanal Matogrossense, the wide seasonally flooded basin of the Paraguay River (Cole 1960, Prance & Schaller 1982, Ratter *et al.* 1988), and in the seasonally flooded savannas of Venezuela (Sarmiento & Monasterio 1971).

The flora of the murundus, in the present case, is mostly composed of a particular subset of species originating from the surrounding cerrado. After comparing these two communities and three other cerrado communities of the region, Oliveira-Filho & Martins (1991) found the highest similarity index for floristic composition between the murundu cerrado and the surrounding cerrado. It is worth noting that only 12 of the 45 species of tall plants surveyed on the mounds were confined to this community, i.e. they were not found in the surrounding cerrado. However, none of these 12 were among the most abundant species of the mound community. Despite presenting this high floristic similarity with the neighbouring cerrado, the murundu cerrado was quite different in community structure. The species of Vochysiaceae, for instance, which were very significant in the surrounding cerrado, were virtually absent from the mounds. On the other hand, *Annona pygmaea*, which is dominant among the low plant community of the mounds, has not been observed elsewhere in the region of Cuiabá. However, as the low plant community was not surveyed in the surrounding cerrado, it is not possible to make quantitative comparisons with the murundu cerrado for such sinusia.

The distance from any mound in the campo de murundus to the margin of the surrounding cerrado is always under 100 m, and this figure can be considered as very short 'mainland-island distance' if compared with other isolated plant communities (e.g. Nilsson & Nilsson 1978, Møller & Rørdam 1985, Rydin & Borgegård 1988). It is also well known that most cerrado woody species are zoochorous, followed by anemochorous species (Gottsberger & Silverbauer-Gottsberger 1983). Thus, one can certainly consider that such distances are short enough for most species to disperse their propagules from the cerrado 'mainland' onto any target mound. A shallow and periodic layer of water around the mounds cannot be considered as a likely hindrance to vertebrates transporting the plant diaspores. In addition, the larger mounds are uniformly spread throughout the campo, so they can operate as stepping stones in the dispersal process, and this usually increases the chance of more propagules reaching the island (MacArthur & Wilson 1967, Møller & Rørdam 1985).

Therefore, it is evident that only a fraction of the cerrado flora around the campo de murundus is able to colonize the islands successfully. This is clearly illustrated by the fact that many seedlings of *Strychnos pseudo-quina* were surveyed on some mounds, but all were found to be dead a few months later. The adult trees of this species were only found in the surrounding cerrado, so they clearly failed to establish successfully on the mounds.

A consequence of the situation whereby only a subset of species are capable of colonizing the mounds/islands is the relatively low species diversity of the

community of tall plants on the mounds (H' = 2.357) when compared with that on the surrounding cerrado (H' = 3.396). This is also shown by the strong concentration of abundance values in few species.

Although the soils of the mounds are not stony and have finer texture and higher amounts of mineral nutrients than those of the surrounding cerrado (Oliveira-Filho 1992), they can only provide the roots with a restricted growing space which is not liable to water-logging. This is certainly a strong limiting factor for many plants that require a larger soil volume without restrictions to the respiration of their root system. The restrictions are more severe for the smaller mounds and also for larger plants. This would explain the predominance of subshrubs in the smallest mounds and the gradient of plant height in the larger mounds, from shrubs at the margins to tall trees at the summit. The distribution of the plant species on the surface of the mounds is also affected by the size and by the convex topography of the mounds which result in a gradient of depth of non-saturatable soil. This gradient is probably short enough to pack the microhabitats for the plant species, so that the partition of the mound surface leads to the clear plant community zonation in topographic belts.

The formation of these particular earthmounds was postulated by Oliveira-Filho (1992) to be a primary succession process in which the mound volume increases mainly as a result of the accumulation of sediments by termite activity. If so, the spatially organized plant community on mounds of increasing size can be also regarded as a set of progressive stages of a plant community succession process that plays an important role in the history of those mounds.

LITERATURE CITED

BROWER, J. E. & ZAR, J. H. 1984. *Field and laboratory methods for general ecology.* Wm. C. Brown, Dubuque.
BUCKLEY, R. 1982. The habitat-unit model of island biogeography. *Journal of Biogeography* 13:69–70.
COLE, M. M. 1960. Cerrado, caatinga and pantanal; the distribution and origin of savanna vegetation of Brazil. *Geographical Journal* 126:168–179.
CONNOR, E. F. & McCOY, E. D. 1979. The statistics and biology of the species-area relationship. *American Naturalist* 113:791–833.
CUNHA, C. N., CAMPOS, M. M. & SILVA, M. Q. 1983. *Estudos biológicos preliminares de uma área de cerrado inundável, transição entre cerrado e pantanal (Mimoso – Santo Antonio do Leverger – MT).* Universidade Federal de Mato Grosso, Cuiabá.
DINIZ de ARAUJO NETO, M., FURLEY, P. A., HARIDASAN, M. & JOHNSON, C. E. 1986. The murundus of the cerrado region of Central Brazil. *Journal of Tropical Ecology* 2:17–35.
EITEN, G. 1972. The cerrado vegetation of Brazil. *The Botanical Review* 38:201–341.
EVERITT, B. 1980. *Cluster analysis.* Halsted, N. York.

FURLEY, P. A. 1986. Classification and distribution of murundus in the cerrado of Central Brazil. *Journal of Biogeography* 13:265–268.

FURLEY, P. A. & RATTER, J. A. 1988. Soil resources and communities of central Brazilian cerrado and their development. *Journal of Biogeography* 15:97–108.

GAUCH, H. G. 1982. *Multivariate analysis in community ecology.* Cambridge University Press, Cambridge.

GENTRY, A. H. 1992. Bignoniaceae, Part 2 (Tribe Tecomeae). *Flora Neotropica Monograph* 25:1–370.

GOODLAND, R. 1971. A physiognomic analysis of the 'cerrado' vegetation of Central Brazil. *Journal of Ecology* 59:411–419.

GOTTSBERGER, G. & SILBERBAUER-GOTTSBERGER, I. 1983. Dispersal and distribution in the cerrado vegetation of Brazil. *Sonderbaende des Naturwissenschaftlichen Vereins in Hamburg* 7:315–352.

HILL, M. O. 1979. *DECORANA – a FORTRAN program for detrended correspondence analysis and reciprocal averaging.* Cornell University, Ithaca.

MACARTHUR, R. H. & WILSON, E. O. 1963. An equilibrium theory of insular biogeography. *Evolution* 17:373–387.

MACARTHUR, R. H. & WILSON, E. O. 1967. *The theory of island biogeography.* Princeton University Press, Princeton.

MATHEWS, A. G. A. 1977. *Studies on termites from the Mato Grosso State, Brazil.* Academia Brasileira de Ciências, Rio de Janeiro.

MATTEUCCI, S. D. & COLMA, A. 1982. *Metodología para el estudio de la vegetación.* General Secretariat of the Organization of American States, Washington.

MØLLER, T. R. & RØRDAN, C. P. 1985. Species numbers of vascular plants in relation to area, isolation and age of ponds in Denmark. *Oikos* 45:8–16.

MUELLER-DOMBOIS, D. & ELLENBERG, H. 1974. *Aims and methods of vegetation ecology.* Wiley, New York.

NILSSON, S. G. & NILSSON, I. N. 1978. Species richness and dispersal of vascular plants to islands in Lake Möckeln, Southern Sweden. *Ecology* 59:473–480.

OLIVEIRA-FILHO, A. T. 1992. Floodplain murundus of Central Brazil: evidence for the termite-origin hypothesis. *Journal of Tropical Ecology* 8:1–19.

OLIVEIRA-FILHO, A. T. & FURLEY, P. A. 1990. Monchão, cocuruto, murundu. *Ciência Hoje* 61:30–37.

OLIVEIRA-FILHO, A. T. & MARTINS, F. R. 1991. Comparative study of five cerrado areas in southern Mato Grosso, Brazil. *Edinburgh Journal of Botany* 48:307–332.

OLIVEIRA-FILHO, A. T., RATTER, J. A. & SHEPHERD, G. J. 1990. Floristic composition and community structure of a Central Brazilian gallery forest. *Flora* 184:103–117.

OLIVEIRA-FILHO, A. T., SHEPHERD, G. J., MARTINS, F. R. & STUBBLEBINE, W. H. 1989. Environmental factors affecting physiognomic and floristic variation in an area of cerrado in central Brazil. *Journal of Tropical Ecology* 5:413–431.

PRANCE, G. T. & SCHALLER, G. B. 1982. Preliminary study of some vegetation types of the Pantanal, Mato Crosso, Brazil. *Brittonia* 34:228–251.

PRESTON, F. W. 1962. The canonical distribution of commonness and rarity. Part I. *Ecology* 43:185–215, Part II. *Ecology* 43:410–432.

RATTER, J. A. 1987. Notes on the vegetation of the Parque Nacional do Araguaia (Brazil). *Notes of the Royal Botanic Garden Edinburgh* 44:311–342.

RATTER, J. A., POTT, A., VALI, J. P., CUNHA, C. N. & HARIDASAN, M. 1988. Observations on woody vegetation types in the Pantanal and at Corumbá, Brazil. *Notes of the Royal Botanic Garden Edinburgh.* 45: 503–525.

RATTER, J. A., RICHARDS, P. W., ARGENT, G. & GIFFORD, D. R. 1973. Observations on the vegetation of northeastern Mato-Grosso I. The woody vegetation types of the Xavantina-Cachimbo Expedition area. *Philosophical Transactions of the Royal Society of London.* B. *Biological Sciences* 266:449–492.

RYDIN, H. & BORGEGÅRD, S-O. 1988. Plant species richness on islands over a century of primary succession: Lake Hjälmaren. *Ecology* 69:916–927.

SARMIENTO, G. & MONASTERIO, M. 1971. *Ecología de las sabanas de America Tropical. Analisis macroecológico de los llanos de Calabozo, Venezuela.* Caracas, Cuadernos Geográficos n. 4.

TÜXEN, R. & ELLENBERG, H. 1937. Der systematische und der ökologische Gruppenwert. Ein Beitrag zur Begriffsbildung und Methodik der Pflanzensoziologie. *Mitteilungen der Florist-soziologischen Arbeitsgeminschaft* 3.